

Novel behavioral responses of sea turtles to gillnet fishing gear

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ABSTRACT

1. Fisheries bycatch, or the incidental capture of non-target organisms, results in high sea turtle mortality and is believed to be a contributor to population declines. Field studies have shown visual stimuli to reduce sea turtle bycatch in gillnets. These studies have focused on bycatch outcomes specific to net-gear modifications and have not explored behavioral mechanisms driving sea turtle entanglement.
2. To study these behaviors, we used wild-caught green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles in controlled tank experiments. We ran binary-choice trials with netted and unnetted passageways in a controlled tank environment. Underwater and overhead cameras recorded initial and subsequent treatment choices in addition to detailed behavior. Trials occurred in daylight, when turtles could presumably see the net. We also recorded time per treatment area, speed and acceleration in the presence of a net, and avoidance behaviors.
3. Turtles reduced their speed in the presence of a net, which suggests that they see and respond to it before each encounter. Both species initially avoided the netted passageway. Avoidance included U-turn and reversal behaviors, which have not been described in previous literature. Green turtles exhibited more U-turn behaviors and net interactions, whereas loggerheads became entangled more frequently.
4. By using controlled experiments with wild-caught animals, we provide novel insights on fine-scale behavioral interactions with fishing gear.

1. Introduction

Fisheries interactions are a leading cause of mortality to sea turtles and other marine species worldwide. Sea turtles are particularly vulnerable because their migratory nature often results in interactions with multiple fisheries and a variety of gear types including but not limited to longlines, trawls, and gillnets (Moore et al., 2009; Finkbeiner

et al., 2011; Senko et al., 2014a, 2014b). Because gillnets are globally ubiquitous and relatively non-selective, this gear results in widespread and frequent bycatch in comparison to other locally distributed and more selective gear types (Lewison et al., 2014). Gillnets are also more commonly used in small-scale fisheries, which often have greater management challenges than industrial-scale fisheries (Peckham et al., 2016).

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Bycatch and the subsequent mortality of sea turtles are a principal driver of sea turtle population declines as it typically impacts numerous juvenile, sub-adult, and adult sea turtles, which have high demographic importance (Heppell, 1998; Bolten et al., 2011). Although sea turtle entanglement in gillnet fisheries has been identified as an important fisheries and conservation issue (Peckham et al., 2007; Alfaro-Shigueto et al., 2011; Finkbeiner et al., 2011; Lewison et al., 2014), few studies have documented sea turtle behavior when interacting with gillnets (but see Galvez et al., 2022). Most bycatch studies assessed turtle-net interactions by catch per unit effort (CPUE) and bycatch per unit effort (BPUE) rather than fine-scale behaviors associated with sea turtle entanglement. Given this lack of behavioral information, it is unclear whether turtles become entangled because: (1) they do not see nets; (2) they see nets but do not perceive them as a barrier; or (3) other variables are driving interactions.

The goal of this study was to document sea turtle behavior in response to gillnets and to compare behavioral responses between two sympatric sea turtle species that frequently interact with gillnet fisheries worldwide – loggerhead sea turtles (*Caretta caretta*) and green turtles (*Chelonia mydas*). We used a binary choice experiment between a netted and unnetted passageway in a controlled environment with underwater and overhead camera recordings to examine both initial and subsequent choices made by each turtle as well as behaviors upon encountering a gillnet. We hypothesized that both species of sea turtles would avoid a netted passageway during daylight hours when they can presumably see the net. We also hypothesized species-specific differences in behavioral responses to gillnet fishing gear given their differences in morphology and life history (e.g., loggerheads may be more likely to become entangled due to a heavier epibiont load, larger head, and less streamlined body).

2. Methods

2.1. Capture and maintenance of turtles

All sea turtles used in this study were a subset of those being captured by Inwater Research Group (IRG) by a dip net, entangling net, or hand capture after entrainment in the intake canal at the St. Lucie Nuclear Power Plant in Jensen Beach, FL. Capture of these turtles was necessary to safely return them to the open ocean, but only a proportion of individuals captured were used in this study due to permitting requirements. For our experimental trials, we only included healthy juvenile green ($n = 16$) and loggerhead ($n = 15$) turtles with a straight standard carapace length (SCL) of 22–78 cm due to logistical limitations related to the size of the experimental tank. After IRG biologists removed a turtle from the canal and collected biometric data, the turtle was kept in a 1.8 m diameter holding tank or in a partitioned section of the larger test tank, both filled with seawater from the canal. We did not hold turtles for >72 h.

2.2. Experimental tank design

We conducted all tank trials in a $13.9 \times 2.3 \times 1.5$ m (length x width x depth) concrete tank beside the intake canal at the St. Lucie Nuclear Power Plant (Fig. 1). A guillotine door, opened by a pulley system, divided a “waiting room” from the treatment area. The treatment area was divided into two passageways through which the turtle could attempt to pass, thus making a choice. Two cameras were mounted above the tank and two were mounted underwater at the end of each passageway within the treatment area to obtain detailed views of turtle movement and specific behaviors (Fig. 2). Both the center divider and side walls of the 2.4 m-long treatment area were painted flat black. The treatment, in this case a modified gillnet, was mounted to a support beam above the divider in the middle of the treatment area (Figs. 1 & 2).

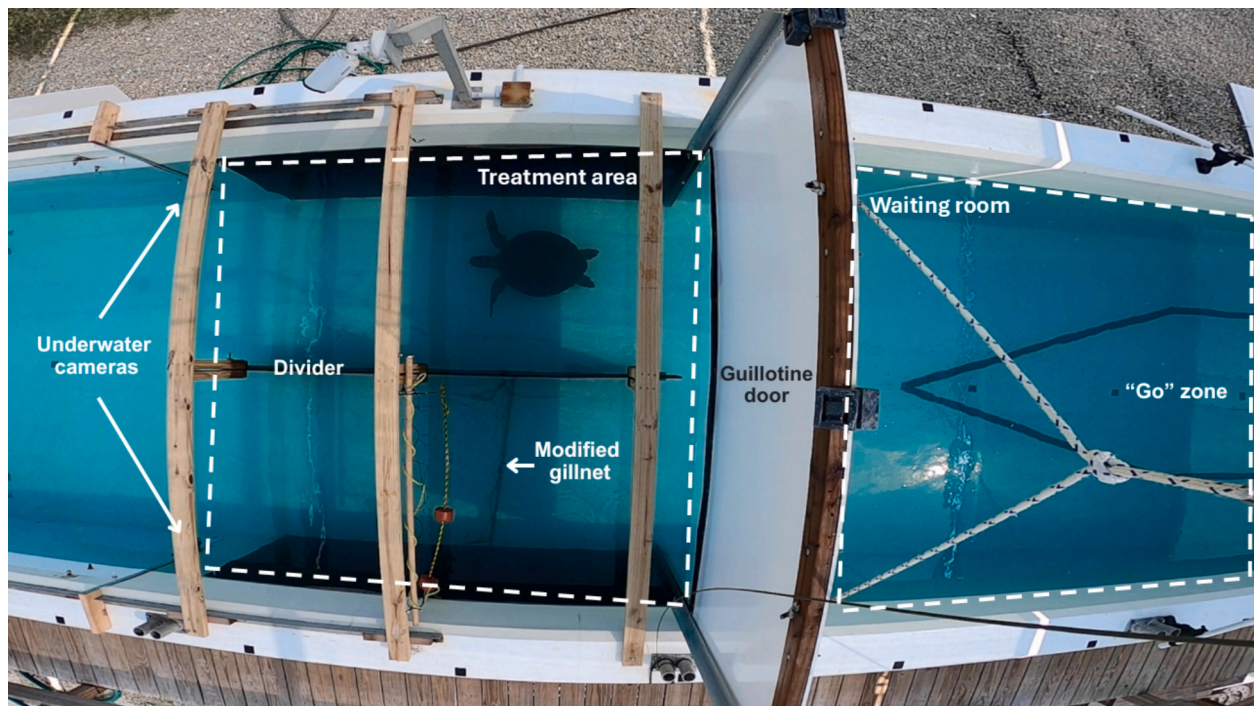


Fig. 1. Experimental tank at the intake canal of the St. Lucie Nuclear Power Plant, Florida, USA. The pentagon on the right side of the tank is the “go” zone within the waiting room where the turtle must be positioned in order for a trial to begin. The upper, netted passageway was the east side of the test tank and the bottom, unnetted passageway was the west side.

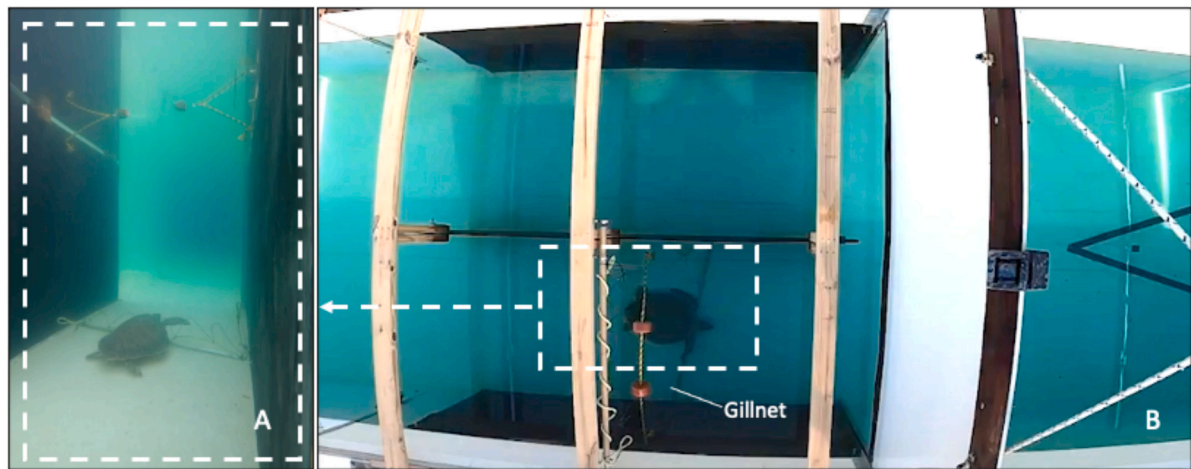


Fig. 2. Underwater (A) and overhead (B) views of the experimental tank during a trial. The treatment in the passageway at the bottom of the picture is a modified gillnet. The subject of this trial is a juvenile green turtle. This is an example of a net interaction because the turtle's head and flipper are through the net. The upper, unnetted passageway is the east side of the test tank and the bottom, netted passageway is the west side. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Accounting for biases in experimental tank

To account for possible directional bias and to attempt to acclimate turtles to the experimental tank before the actual trials, each turtle was placed in the experimental tank with the guillotine door open and no treatments in the treatment area for 20 min. A recording of this acclimation period was viewed to count how many times the turtle chose the two trial passageways and was later compared with directional choices during the trial using a two-proportions z-test. We waited to start each trial until the turtle was positioned closer to the center of the tank, in the “go” zone (right side of Fig. 1), rather than against either wall to avoid the possibility of the turtle swimming into a treatment passageway solely based on where it was first positioned when the guillotine door was raised rather than choosing of its own volition.

2.4. Behavioral trials

We conducted trials year-round between September 2020 and October 2021 during daylight hours (between 1 h after sunrise and a half hour before sunset). Each turtle was put through three consecutive two-choice trials, which enabled later analysis of potential learning effects. However, only the first trial was addressed in this study to ensure independent behaviors. Turtles were moved from a 1.8 m holding tank into the larger experimental tank (Fig. 1) and given 1 min to calm, passing the period of collisions and direction changes resulting from placement into the tank. Video recording began prior to the turtle being transferred to the experimental tank. From a hidden position, we then watched the video for the turtle to swim into the “go” zone with at least half of its body in the pentagon and head orientation generally facing the door. When the turtle was correctly positioned, the door was raised, revealing the treatment area with one passageway containing a modified gillnet and one passageway being open, which created a choice between netted and unnetted passageways. We measured latency as the time between the door opening and when the turtle crossed into the treatment area (Table I). Each 15-min (900 s) trial began as soon as the turtle's head crossed under the door. We monitored the trials from out of the turtle's line of sight so that we could quickly remove the turtle if it became entangled for >20 s (Entanglement; Table I), which terminated the trial. We aborted the trial when turtles either failed to enter the “go” zone within 30 min of being placed in the tank or failed to enter the treatment area within 30 min of the door opening.

Table I

Observed behaviors with definitions and measures unique to this study and the corresponding statistical models used to analyze them.

Observed behavior	Definition	Measure	Statistical model
Latency	Time from door opening to turtle entering the treatment area (head crossing under door)	Duration	Generalized linear model (negative binomial)
Breath	Turtle raising its head above the water's surface	Count	Generalized linear model (negative binomial)
Collision	Turtle's head or shoulder making direct contact with wall or divider without an attempt to slow	Count	Generalized linear model (Poisson)
Reversal	Moving backwards while maintaining a forward orientation	Count	Generalized linear model (negative binomial)
U-turn	180-degree pivot in under 10 s	Count	Generalized linear model (Poisson)
Net interaction	Head or at least one flipper through the net with directional tension on net (lead line moves) for <20 s	Count	Generalized linear model (Poisson)
Entanglement	Net interaction lasting for 20 s or more (trial terminated and turtle disentangled immediately)	Binary occurrence and duration before	Cox proportional hazards test

2.5. Behavior measurements

We analyzed the behaviors exhibited by each turtle using recordings from four camera views. We measured the amount of time it took turtles to enter the treatment area after the door opened (latency), how much time turtles spent in each area of the tank, how many times turtles breathed per trial, how many times turtles collided with walls or the divider, which passageway of the treatment area turtles chose first, and the frequency of choosing each passageway for the duration of the trial. Breath, Collision, and Entanglement were recorded as instantaneous

events whereas the rest of the behaviors of interest were recorded as durations (Table I). We used a visual object tracking algorithm to automatically measure the turtle speed, acceleration, and angle of approach. A previous study (Reavis et al., 2021) has shown the success of the SiamMargin (Kristan et al., 2019) method for this specific application. Therefore, we used this algorithm to estimate the exact location of the turtle's head throughout the image frames. Using calibration points marked on the tank, we applied a transformation to convert the pixel positions on the image plane to relative position values in metric units. Thus, the calibration step enabled us to estimate the speed and acceleration of the turtle in m/s and m/s² respectively. For those measurements, we recorded from the turtle's head crossing into a netted treatment area until just before the turtle made contact with the net. For each net interaction, we also recorded the same measurements in 1 min of the waiting room, away from the net, as a control (O'Connell et al., 2014). We initially intended to collect control measurements in the unnetted passageway, but turtles did not reliably swim through that passageway.

2.6. Statistical analysis

We used a binomial test to test the null hypothesis that the turtles show no preference between netted and unnetted passageways, both for the first choice, which is the only independent choice, and total choices between the netted and unnetted passageways for all turtles included in the study. We used Z tests to compare the proportion of green and loggerhead turtles that chose the netted passageway.

A Shapiro Wilks test and a Levene test showed that time per passageway of both species was not significantly skewed from a normally distributed and had equal variance, respectively, so we used a *t*-test to compare the amount of time turtles spent in the netted passageway to the time spent in the unnetted passageway. After partitioning the data by species, a Shapiro Wilks test showed that it did not fit a normal distribution, so we conducted a Kruskal-Wallis Rank Sum test to compare the time spent per passageway between green and loggerhead turtles. We used survival analysis (Cox proportional hazards regression model; 'coxph' function in the R package 'survival') to assess differences in the survival, or in this case non-entanglement, of green and loggerhead sea turtles (Cox, 1972). Trials were concluded after 900 s if no entanglement occurred, so the survivorship curve is right-censored. Then we used a generalized linear model with a negative binomial distribution to compare latency behavior between species (Table I; Stoklosa et al., 2022). We used a Chi-square goodness-of-fit test to determine the correct error distribution (i.e., Poisson vs. negative binomial) for each generalized linear model.

Given that entanglement resulted in a trial being terminated before 900 s and unequal sampling time among turtles, we offset all models of behavioral events by the log of the total trial duration (in seconds). We used a generalized linear model with a Poisson distribution to compare the number of net interactions between green and loggerhead turtles. We used a Z-test to determine if a larger proportion of green or loggerhead turtles were entangled. We separated size tests by species due to sampled loggerheads generally having a larger straight carapace length (average SCL = 62.6, SE = 1.85) than sampled green turtles (average SCL = 44.6, SE = 4.07). We partitioned the data by species and performed separate generalized linear models with a binomial distribution to determine if size affected likelihood of entanglement.

We also used generalized linear models with an offset for trial duration to compare the number of U-turn behaviors and Reversal behaviors (Table I), with a Poisson and negative binomial distribution, respectively, exhibited by green and loggerhead turtles. We conducted separate linear models for both species with an offset for trial duration to determine if turtle size influenced the number of U-turn behaviors and Reversal behaviors (Table I) exhibited. We used a generalized linear model with a Poisson distribution to compare the number of collisions with the walls between the species and another generalized linear model

with a negative binomial distribution to compare the number of breaths taken between species.

To create a predictive model of how speed, acceleration, and angle of approach may affect turtle entanglement, we used a generalized linear mixed effects model (GLMER) from the R package lme4 (Bates et al., 2015) with a binomial error distribution and included turtle identity as a random effect (Kimbell and Morrell, 2016). To determine whether turtle speed is affected by net presence, we created a null linear mixed effects model with turtle identity as a random effect, and then we compared it to an identical model with the exception of net presence being added as a fixed effect. These models were compared using a Chi-square goodness-of-fit test. We replicated these tests, changing the independent variable to species, to determine if speed, acceleration, or angle of approach differed between species. Means are reported with standard error. Statistical significance was inferred at a *p*-value of 0.05. All analyses were conducted using R (version 4.4.0). Graphical figures were created using the R package ggplot2 (Wickham, 2016).

3. Results

3.1. Directional bias

The proportion of choices of the eastern and western (top and bottom in Fig. 1) treatment passageways was significantly different between the acclimation period, when no nets were present, and the trial period, when one passageway contained a net (Two-proportions *z*-test: $z = 11.5$, $df = 59$, $p < 0.001$), implying that turtle choice was affected by treatment presence rather than prior directional bias.

3.2. Choices

For the first and only independent choice, turtles chose the netted passageway significantly fewer times than the unnetted passageway (binomial test: $x = 8$, $n = 31$, $p = 0.01$), and this first choice did not differ between green and loggerhead turtles (Fig. 3; Z-test: $df = 1$, $z = 0.30$, $p = 0.76$). We found no significant difference in total choices between a netted and unnetted passageway (binomial test: $x = 69$, $n = 151$, $p = 0.32$), and our data do not show an effect of species on total choices (Z-test: $df = 30$, $z = 5.9$, $p = 0.25$).

3.3. Time

The average time spent in the netted and unnetted passageways did not differ significantly overall (*t*-test: $t = 0.17$, $df = 30$, $p = 0.86$) or between species (Kruskal-Wallis: $X^2 = 0.19$, $df = 1$, $p = 0.66$). The total duration of loggerhead trials (average duration = 365 s, SE = 77) was significantly shorter than the total duration of green turtle trials (average duration = 759 s, SE = 77 Cox proportional hazards test: $df = 1$, $z = -3.1$, $p = 0.002$; Fig. 4). Trial duration is associated with entanglement because the only reason trials were terminated before 900 s was when entanglement occurred (Fig. 4). Green turtles exhibited significantly longer latency (average latency = 176 s, st. error = 74) than loggerhead turtles (average latency = 49 s, SE = 14) with latency measured as the time between the treatment area being revealed and the turtle leaving the waiting room to enter the treatment sector (GLM: $p = 0.001$, family = negative binomial).

3.4. Net interaction

Due to the difference in trial duration between species (Fig. 4), we offset all models of behavioral events by the log of the total trial duration. With this offset, our data show that green turtles exhibit significantly more net interactions (average net interactions = 3.69, SE = 1.46) than loggerhead turtles (average net interactions = 1, SE = 0.29; Fig. 5; GLM: $p = 0.047$, family = poisson). However, loggerhead turtles are entangled significantly more than green turtles (Fig. 4; Z-test: $z = 3.8$, df

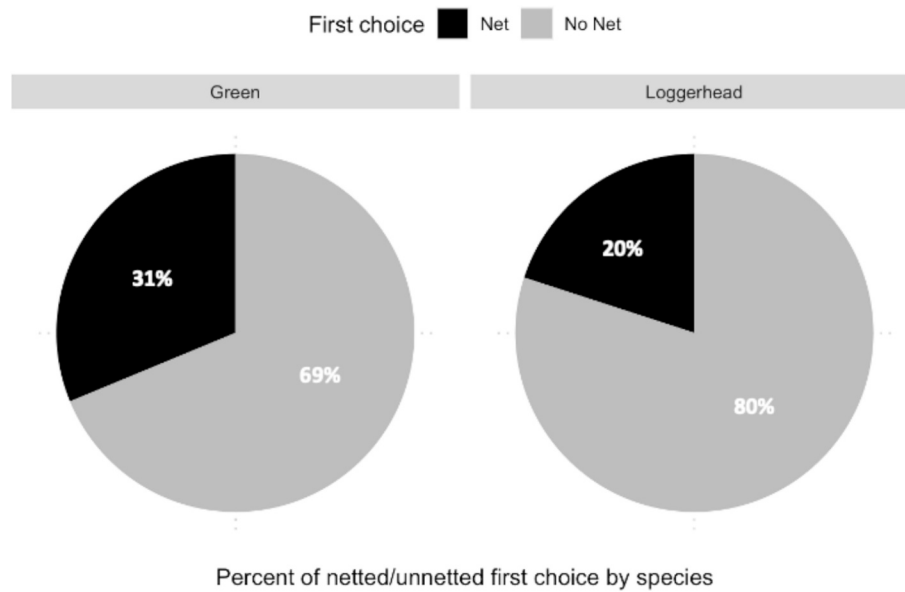


Fig. 3. Proportion of green ($n = 16$) and loggerhead ($n = 15$) turtles that chose the netted and unnetted passageways for their first choice. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

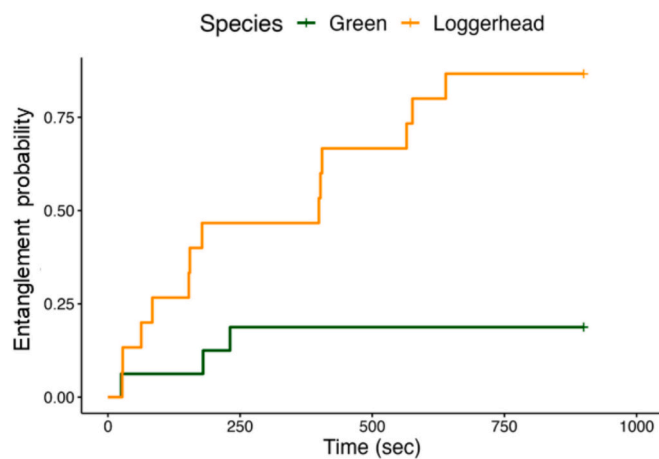


Fig. 4. Survival curve showing likelihood of entanglement for green ($n = 16$) and loggerhead ($n = 15$) turtles over a 15-min (900 s) trial. Figure shows percentage of entangled turtles over time. The crosses represent censored data because all trials were terminated at 900 s if no entanglement occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$= 1, p < 0.001$). Entanglement occurrence was not significantly different by size (SCL) for loggerhead (GLM: $p = 0.56$, family = binomial) or green turtles (GLM: $p = 0.14$, family = binomial).

3.5. Avoidance and disentanglement behaviors

With an offset for trial duration, green turtles exhibited significantly more U-turn behaviors per trial (average U-turns = 3.31, st. error = 1.19) than loggerhead turtles (average U-turns = 0.13, st. error = 0.13; Fig. 5; GLM: $p < 0.001$, family = poisson). Size (SCL) had no significant effect on how many U-turns both green (linear model: $t = 0.14, p = 0.89$) and loggerhead turtles (linear model: $t = 0.62, p = 0.55$) exhibited in each trial. With the same offset, there is no significant difference in the number of reversal behaviors exhibited by each species (Table II; Fig. 5; GLM: $p = 0.17$, family = negative binomial). However, the number of reversals, offset by trial duration, by both green (linear model: $t =$

$-4.04, p = 0.001$) and loggerhead turtles (linear model: $t = 2.44, p = 0.03$) differed by turtle size (SCL), with smaller turtles exhibiting more reversals than larger turtles.

3.6. Collision and breath

When trial duration is accounted for with an offset, green turtles (average collisions = 0.81, SE = 0.52) collided with walls of the tank and passageway divider significantly fewer times per trial than did loggerhead (average collisions = 0.87, SE = 0.41) turtles (GLM: $p = 0.04$, family = poisson). With the same offset, green turtles took significantly more breaths (average breaths = 2.63, SE = 0.72) per trial than loggerhead turtles (average breaths = 0.40, SE = 0.29).

3.7. Speed, acceleration, and approach angle

We found that speed, acceleration, and angle of approach were not significant predictors of turtle entanglement (GLMER: $df = 1; z = -0.20, -1.9, -1.3; p = 0.84, 0.06, 0.18$). When comparing a linear mixed effects model with the effect of net presence/absence on speed to a null model, the model that includes net presence/absence is significantly different than the null model, showing that speed is significantly slower in the presence of a net (average = 0.23 mps, SE = 0.012) than in an area without a net (average = 0.29 mps, SE = 0.012) (Chi-squared goodness of fit test: $X^2 = 22.62, df = 1, p < 0.001$). Using the same method for acceleration, we found that the model including net presence/absence is significantly different from the null model (Chi-squared goodness of fit test: $X^2 = 6.5, df = 1, p = 0.01$). Turtles exhibited less acceleration in the presence of a net (average = 0.0012 mps, SE = 0.004) than in the absence of a net (average = 0.013 mps \pm 0.003). Speed, acceleration and angle of approach did not significantly differ by species (Chi-squared goodness of fit test: $X^2 = 0.46, 1.22, 0.11; df = 1; p = 0.45, 0.27, 0.74$).

4. Discussion

Our use of controlled binary choice trials with two sea turtle species provides unique insight into sea turtle behaviors associated with fishing nets. We documented the existence of multiple net-avoidance behaviors (e.g., U-turns and reversals), the frequency of which was species dependent. Although both species initially avoided the netted

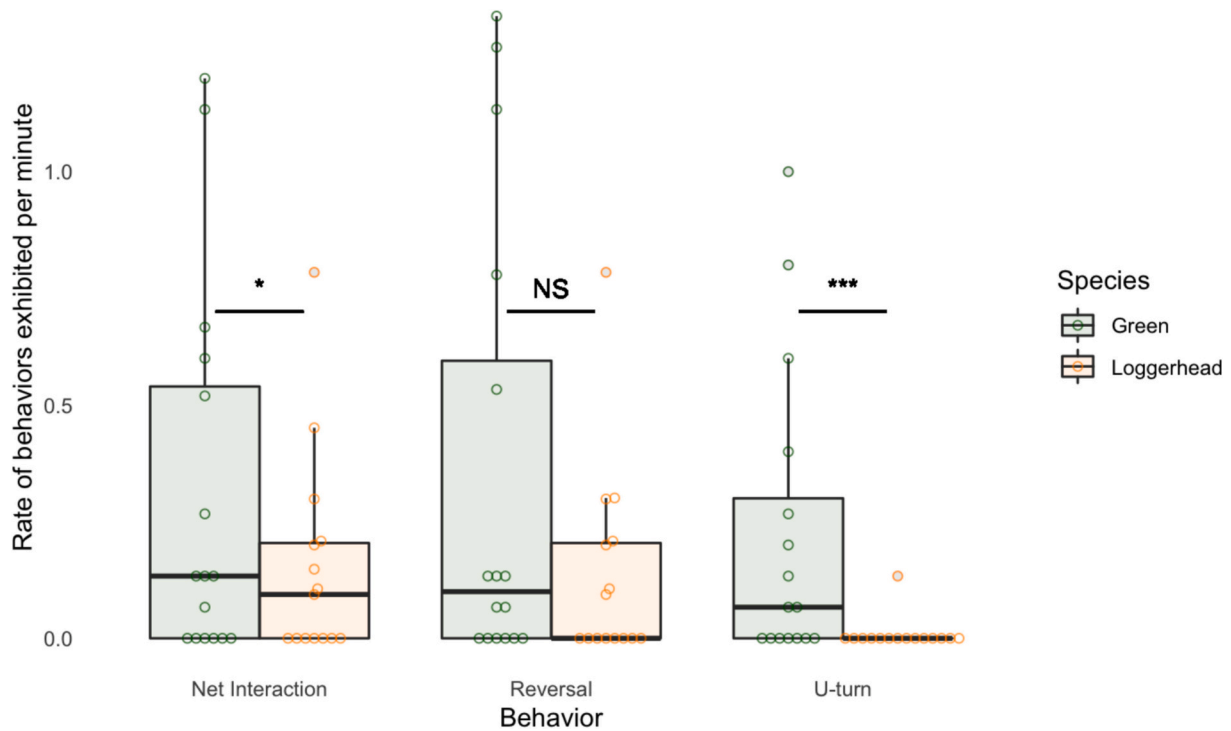


Fig. 5. Rate of net interactions and avoidance behaviors per minute by green ($n = 16$) and loggerhead ($n = 15$) turtles. One asterisk denotes a statistically significant difference between green and loggerhead turtles at $p < 0.05$ and three asterisks denote a p -value < 0.001 as derived from a generalized linear model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table II

Summary of generalized linear models used to compare the differences in behavioral events between green and loggerhead sea turtles. Average number \pm standard error. All models of behavioral events were offset by the log of total trial duration in seconds to account for uneven sampling time. Significant differences are indicated with an asterisk.

Test	Greens	Loggerheads	p-value	Distribution
Latency (sec)	175.9 \pm 73.92	48.8 \pm 13.83	0.001**	Negative binomial
Trial duration (sec)	758.5 \pm 76.68	364.9 \pm 77.4	0.002**	N/A
Number of net interactions	3.69 \pm 1.46	1 \pm 0.29	<0.001***	Poisson
Number of u-turns	3.31 \pm 1.19	0.13 \pm 0.13	<0.001***	Poisson
Number of reversals	3.69 \pm 1.49	0.87 \pm 0.27	0.17	Negative binomial
Number of collisions	0.81 \pm 0.52	0.87 \pm 0.41	0.04*	Poisson
Number of breaths	2.63 \pm 0.72	0.40 \pm 0.29	0.04*	Negative binomial

passageway, green turtles were more likely to repeatedly interact with nets, while loggerheads were more likely to become entangled. There were often multiple net interactions and avoidance behaviors preceding actual entanglement, which suggests that there may be multiple levels of interaction with gillnets in addition to entanglement occurrence in fisheries.

Both species initially chose the netted passageway significantly less than the unnetted passageway but there was no significant difference in total choices. It is possible that turtles avoid the net initially because it is a “novel” object (Lamont and Johnson, 2021). By novel, we are referring to ecological novelty (Robertson et al., 2013) as opposed to ontogenic novelty (Reger et al., 2009). Although there is no way to determine how many gillnets a turtle has encountered in its lifetime, it is unlikely that nets have persisted long enough to elicit trait changes (Darimont et al.,

2009). Many of the turtles in this study were removed with an entangling or dip net after being entrained in a power plant intake canal where entangling nets are set for eight to 10 h per day (Bresette et al., 2005). It is possible that turtles initially avoided the netted passageway because of a “novel” object effect or due to prior net experience (Frost et al., 2007). The exploratory nature of green turtles (Kudo et al., 2021) might be expected to result in turtles choosing a novel object first, unless that object is perceived as a barrier or a risk. While initial avoidance of the net by the turtle suggests detection of the net, it is difficult to discern whether this indicates object detection or risk detection as we did not test a control that could show how turtles interact with an object that did not represent a hazard.

Entanglement and U-turn occurrence did not vary by size (SCL), but smaller green and loggerhead turtles both exhibited more reversals than larger turtles. It is important to note that larger turtles still exhibited reversal behaviors even if the rate was lower than smaller turtles. We suspect this may be more of a function of passageway size than of maneuverability of larger turtles because each passageway was only 1.2 m wide, and adult sea turtles are known for their mobility and maneuverability despite their large body size (Pimiento et al., 2020).

Choosing both netted and unnetted passageways after initially avoiding the netted passageway may be the result of habituation. Prolonged exposure to an object or hazard decreases an animal's vigilance (Uchida et al., 2019; Schakner and Blumstein, 2013). Even if turtles in this study interacted with the net and were not fully entangled, this did not necessarily prevent future interactions with the net. It would have been informative to test whether turtles are more likely to avoid the netted sector after an entanglement, but for animal safety reasons, we terminated such trials to remove the turtle from the net. We point out differences between a controlled trial in a test tank and a turtle interacting with a net in the open ocean. Turtles in this study were guaranteed prolonged exposure to the net because of the small size of the test tank and the turtles' inability to escape from the proximity of the net; however, in the ocean, a turtle's initial net avoidance can result in it swimming away and not approaching the net again.

Our findings suggest that while avoidance and disentanglement behaviors such as reversals and U-turns can prevent entanglement, not all efforts are successful, as some entanglements persist despite repeated attempts at disentanglement. Each net interaction can be considered a “near-miss” (Van der Schaaf et al., 2013), whereby a sequence of events (e.g., a turtle swimming towards a gillnet) has risk of entanglement. Previous gear modification studies have used bycatch per unit effort (BPUE) as a metric for how hazardous gillnets and other fishing gear are to sea turtles, but our trials suggest that for every known entanglement there may be numerous near-miss net interactions that never result in entanglement. An analytical framework incorporating risk inherent in near-misses has effectively guided risk reduction in the human safety and medical fields (Henneman and Gawlinski, 2004; Mutic et al., 2010), nuclear power industry (Gnoni and Saleh, 2017), and aviation (Tiller and Bliss, 2017). Similar analyses describing risk to turtles from near-misses with nets might be helpful in understanding net-entanglement mortality and methods to reduce this risk.

We found species-based differences in net interactions with green turtles exhibiting significantly greater frequency of net interactions and U-turns than did loggerheads (Fig. 5). Loggerheads became fully entangled more frequently than green turtles (Fig. 4). Combined, these data show that loggerheads tend to become entangled after fewer near-miss interactions than do green turtles, suggesting that previous studies of loggerhead bycatch may better represent the number of turtles

interacting with gillnets than green turtles, although we acknowledge this is speculative.

We analyzed sea turtle movement in terms of speed, acceleration, and angle of approach related to the net. Speed and acceleration were both significantly slower in the netted passageway than the waiting room. While approaching a net indicates a choice, lower speed and acceleration demonstrates a response bias (Fletcher et al., 2013), likely due to detection of the net, indicating object detection as opposed to risk detection which would likely elicit avoidance rather than a slower approach. This is evidence against the assumption that turtles become entangled in nets during the day because they do not see them. We hypothesized that a slower approach would reduce entanglement probability, but did not find that speed, acceleration, or angle of approach were significant predictors of entanglement in our experiments. It is possible that a slower approach may result in a reduced entanglement probability in a fishery but not in experimental conditions where turtle swimming speed may be different than in the ocean. If turtles are in fact approaching visible nets more slowly in a natural setting, this might translate to approaching an artificially illuminated net more slowly during nighttime.

After subtracting the time turtles were entangled or were interacting with the net, time spent per passageway was not significantly different between the unnetted and netted passageways. Physical contact with the nets impeded turtle movement, so including durations of net interaction

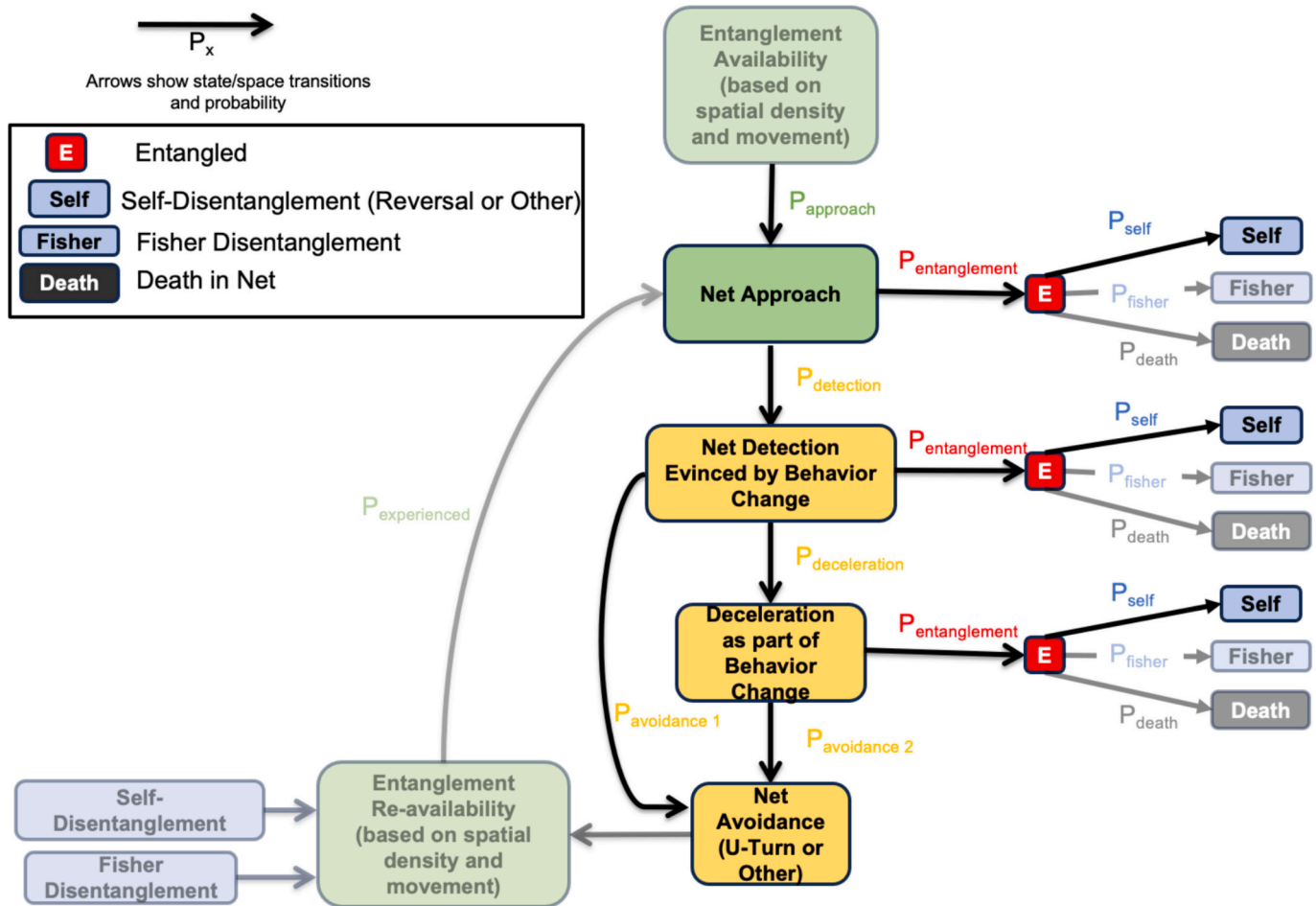


Fig. 6. An event-chain model describing probabilities of event transitions leading to sea turtle catch in net fisheries. The conceptual model outlines multiple discrete opportunities to affect outcomes by reducing turtles' probabilities of net approach, net detection, swimming-behavior change, net avoidance, and re-availability for entanglement influenced by learning effects. The model also describes probabilities of self- and fisher-disentanglement, which are expected to be a function of entanglement severity and location within the net. The present study contributes data to this framework. With complete information, the model can identify steps that may have the greatest impact on reducing bycatch mortality. Without full information, the model remains useful in outlining the diversity of bycatch-reduction methods available to fisheries managers.

or entanglement would not be an accurate representation of intentional time spent in the areas. By contrast, latency and trial duration were significantly different between species. Green turtle trials lasted significantly longer because most green turtles did not become entangled, meaning their trial lasted the full 15 min, whereas loggerhead trials lasted an average of 6 min because of entanglement and subsequent termination of the trial (Table II; Fig. 4).

Our findings suggest that entanglement may be the culmination of a chain of events with unique causes and probabilities; thus, we present a conceptual event-chain model that provides a framework for understanding the mechanisms that may lead to sea turtle bycatch in net fisheries (Fig. 6). Each event may affect the overall probability of entanglement, where interactions preceding entanglement are near misses that provide an opportunity to shape bycatch mitigation (Fig. 6). If a deterrent is not strong enough to prevent turtles from interacting with gillnets (lower P_{approach} ; Fig. 6), then it might be beneficial to modify gear in a way that reduces the probability of entanglement, such as escape panels on pound nets (Ishihara et al., 2011). Alternatively, buoyless nets, which have shown to reduce sea turtle bycatch in fishery experiments, could enable turtles to swim over nets instead of becoming entangled (Peckham et al., 2016). In addition to mechanical solutions like escape panels or buoyless nets, sensory-based approaches such as visual cues (e.g., net illumination) may allow turtles to not only see nets ($P_{\text{detection}}$) but also recognize them as risks, thereby responding by potentially changing velocity ($P_{\text{deceleration}}$), reducing the extent of entanglement, and more easily evading entanglement (increase $P_{\text{avoidance}}$; Fig. 6); however, change in velocity or avoidance behavior may only indicate detection ($P_{\text{detection}}$). Combinations of net modifications affecting multiple levels of interactions could apply to event probabilities for detection ($P_{\text{detection}}$), initial interaction (P_{approach}), subsequent interactions ($P_{\text{experienced}}$), and ability to escape (P_{self}) with the goal of reducing entanglement ($P_{\text{entanglement}}$) and mortality (P_{death} ; Fig. 6).

Our trials indicate that green turtles are less likely to become entangled in gillnets in this controlled setting, but studies show that bycatch is a threat to both green (López-Barrera et al., 2012; Mancini et al., 2012; Senko et al., 2014b; Ortiz et al., 2016) and loggerhead turtle populations (Peckham et al., 2008; Murray, 2009; Echwikihi et al., 2012; Senko et al., 2017). Alfaro-Shigueto et al. (2011) demonstrated entanglement of both species in gillnet and longline fisheries, suggesting that differences in species-specific bycatch rates could be attributed to varied habitat use as opposed to behavioral differences. More frequent net interactions by green turtles indicate that green turtles return to nets repeatedly, even after extracting themselves from the net with reversal behavior, thus repeating the risk of entanglement, albeit potentially at a lower probability. Repeated interactions also suggest object detection but not risk detection by green turtles since they are actively interacting with the net as opposed to avoiding it. Sea turtles may perceive the net, at least initially, as something that is a hindrance to travel but not a risk of entanglement, so they attempt to push through it. In the ocean, both species frequently encounter and interact with *Sargassum*, naturally occurring seaweeds that float in island-like masses (Phillips et al., 2025). The turtles can push through *Sargassum* without the risk of entanglement. In our study, the turtles may perceive the net as an object similar to *Sargassum*, not realizing the risk of entanglement. However, after repeated near entanglements (and subsequent disentanglement), green turtles may perceive net interactions as a risk. In contrast, loggerhead risk is more associated with an increased likelihood to become entangled on an initial or early encounter with a net, possibly due to a heavier epibiont load (Pfaller et al., 2008; Fuller et al., 2010), larger head, and less streamlined body that make it more difficult to self-disentangle from monofilament mesh (decreased P_{self} and increased P_{death} ; Fig. 6). Interspecific differences in predator avoidance, or escape ability, may also contribute to differences in behavioral responses to gillnets as green turtles have been shown to evade shark bites more than loggerheads due to their greater speed and maneuverability (Heithaus et al., 2002; Wirsing et al., 2008).

We acknowledge that our study was conducted in a controlled environment that cannot replicate real-world fisheries. Our gillnet was 1.2 m wide to be able to fit in one side of our binary choice setup, whereas fisheries typically use 400 m to 2 km of nets (Peckham et al., 2007, 2016; Senko et al., 2022). Gillnets also differ regionally, seasonally, and by fishery; therefore, our green monofilament gillnets might be more or less detectable than other net variations. Moreover, gillnets likely even vary within the same fishery, as different fishers may use gillnets made out of different materials and sizes, with additional differences in age and wear levels of netting material, all of which may affect visual detection and catch efficiency. Finally, our turtles were unable to swim away from the presented nets entirely, which is usually possible in the open sea. Nevertheless, loggerheads interacting with monkfish gillnet fisheries in North Carolina showed net avoidance behaviors similar to those in this study (Galvez et al., 2022). The monkfish gillnet study was conducted on a day with high visibility and low turbidity, similar to the conditions in our controlled trials, indicating that these behaviors have not yet been documented in high turbidity (Galvez et al., 2022). We acknowledge that other variables including environmental factors, net content (target catch), and seasonality may play a role in bycatch, but we did not replicate those factors as our goal was to create a baseline understanding of sea turtle behavior with naturally visible gillnets that may then inform bycatch reduction practices such as net illumination or other net modifications.

CRediT authorship contribution statement

Janie L. Reavis: Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Blair E. Witherington:** Methodology, Funding acquisition, Conceptualization, Writing – review & editing. **Michael J. Bresette:** Resources, Project administration, Funding acquisition. **Kinley Ragan:** Investigation, Writing – review & editing. **John H. Wang:** Funding acquisition, Writing – review & editing. **Stephen C. Pratt:** Methodology, Formal analysis, Data curation, Conceptualization, Writing – review & editing. **H. Seckin Demir:** Formal analysis, Data curation. **Jennifer Blain:** Software, Resources. **Sule Ozev:** Software, Resources. **Dale F. DeNardo:** Project administration, Methodology, Funding acquisition, Conceptualization, Writing – review & editing. **Jesse F. Senko:** Resources, Project administration, Methodology, Funding acquisition, Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known conflicts of interest that could have appeared to influence the work reported in this paper.

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Data availability

The data is shared at https://osf.io/fmzg8/?view_only=c39cc63a24984677907776d02148ca61.

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